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North American Triclad Turbellaria, 17: Freshwater Planarians From Lake Tahoe[1]

By Masaharu Kawakatsu[2]

The present paper is concerned with the taxonomy and chorology of two freshwater planarians that occur in Lake Tahoe in the Sierra Nevada Mountains of California and Nevada. Bottom samples of planarians were collected in 1962 and 1963 during the California-Nevada Tahoe Fisheries Study made by the staffs of the California Fish and Game Department and the Nevada Fish and Game Commission.

According to communications from Mr. Ted C. Frantz, Lake Tahoe Fisheries Manager, planarians were taken with a 6-inch Ekman dredge in depths of less than 500 feet and with a 9-inch modified Ekman dredge from 600 to 1640 feet. Planarians collected were first relaxed in epsom salts, then fixed on the spot in 99 percent isopropyl alcohol. Forty vials of specimens were obtained (22 vials of the 1962 material and 18 vials of the 1963 material). The collection consists of about 250 specimens and includes two species. Examination with a binocular microscope shows that a considerable number of the planarians were in a sexually mature state.

The first pigmented planariid species in the material is a new subspecies of *Phagocata nivea* Kenk, 1953, a species hitherto known only

[1] Continuation of a series by L. H. Hyman (see "References").

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from Alaska. The second species, of which only two specimens are available, one sexual and the other asexual, is a dendrocoelid. A series of sections of these animals showed that this is an undescribed species of the genus *Dendrocoelopsis* Kenk, 1930.

The 1962 material of the Lake Tahoe planarians was sent first by the collector for identification to Dr. L. H. Hyman of the American Museum of Natural History. It was, however, returned to me by Dr. Hyman herself, who told me that her declining health did not permit her to continue taxonomic work. The 1963 material was presented to me by Mr. Frantz upon my request. He also provided me with the detailed data of collections of the Lake Tahoe bottom samples, some notes on living material, and several publications about the lake.

I wish to express my hearty thanks to Dr. Libbie H. Hyman not only for giving me the rare opportunity of studying these valuable materials but also for kindly permitting me to continue her excellent serial work "North American Triclad Turbellaria" (see "References"). She also gave me much valuable criticism. I am indebted to Mr. Ted C. Frantz and his co-workers (Messrs. A. J. Cordone, D. Weidlein, S. Davis, R. Wickwire, S. Nicola, J. Curran, N. Saake, R. Hauswald, V. Keefer, M. Arnold, and B. Zorko) for the gift of the present collections. I owe much to Dr. Roman Kenk and to Professor Atsuhiko Ichikawa for their interest in the work and to Dr. Marie M. Jenkins for some pertinent literature and for correction of my English manuscript.

This paper is affectionately dedicated to Dr. Libbie Henrietta Hyman, an old specialist of turbellarians.

ABBREVIATIONS USED IN FIGURES.—bc=bulbar cavity; bs=bursa stalk; cb=copulatory bursa; ca=common antrum; cg=cement glands; cod=common ovovitelline duct; e=eye; ed=ejaculatory duct; gp=genital pore; i=intestine; ia=intestinal anastomosis; m=mouth; ma=male antrum; o=ovary; od=ovovitelline duct; pb=penis bulb; pg=penis glands; ph=pharynx; pp=penis papilla; sd=sperm duct; sv=spermiducal vesicle; t=testis; v=vagina; yg=yolk gland.

LIST OF LOCALITIES.—The original vial numbers were rearranged according to the division of counties and states of the localities (see fig. 1). Stations 1–24 are located in California in the western two-thirds of the lake area; 25–40 are located in Nevada in the eastern third of the lake area. The number following each station number indicates the specimen lot number as it was registered in my fixing notebook. The information following this number is the data found on the labels of the vials, together with my own notes made from examination of the specimens. Four lots of specimens (nos. 5, 23, 30, 32) that I received from Dr. Hyman were already dry.

No. 1. Specimen Lot No. 477. South Tahoe, Eldorado County, California. Depth, 15 to 16 feet. Oct. 17, 1963. Six asexual specimens of *Phagocata*. Coll. Frantz.

No. 2. Lot No. 475. South Tahoe, Eldorado County, California. Depth, 85 to 99 feet. Aug. 14, 1963. One sexual (No. 475a; slides) and 1 asexual specimen and 2 fragments of *Phagocata*. Coll. Frantz and Saake.

No. 3. Lot No. 453. South Tahoe Shelf, Eldorado County, California. Depth, 21 to 405 feet. Aug. 20, 1962. Eight asexual specimens and 3 fragments of *Phagocata*. Coll. Frantz, Curran, and Saake.

No. 4. Lot No. 460. South Tahoe Shelf, Eldorado County, California. Depth, 248 to 448 feet. Dec. 9, 1962. One sexual specimen with cocoon (No. 460a: whole mount) and about 20 fragments of *Phagocata*. Coll. Frantz, Curran, and Saake.

No. 5. Lot No. 446. Emerald Bay, Eldorado County, California. Depth, 116 to 198 feet. July 11, 1962. One asexual specimen (No. 446a: slides) of *Phagocata*. Coll. Frantz, Curran, and Saake.

No. 6. Lot No. 484. Emerald Bay, Eldorado County, California. Depth, 190 to 203 feet. Dec. 22, 1963. Four asexual specimens of *Phagocata*. Coll. Frantz.

No. 7. Lot No. 449. Sugar Pine Point, Eldorado County, California. Depth, 19 to 229 feet. July 18, 1962. Two asexual specimens and 2 fragments of *Phagocata*. Coll. Frantz, Curran, and Saake.

No. 8. Lot No. 464. Tahoma, Placer County, California. Depth, 213 feet. Dec. 21, 1962. Two sexual but not fully mature (No. 464 b, c: slides) and 23 asexual (No. 464a, d: slides) specimens and 2 fragments of *Phagocata*. Coll. Frantz and Curran.

No. 9. Lot No. 463. Tahoma, Placer County, California. Depth, 439 to 460 feet. Dec. 21, 1962. One sexual but not fully mature (No. 463a: slides) and 1 asexual (No. 463b) specimen of *Phagocata*. Coll. Frantz and Curran.

No. 10. Lot No. 472. McKinney Bay, Placer County, California. Depth, 17 to 20 feet. June 12, 1963. One sexual specimen and 1 fragment of *Phagocata*. Coll. Frantz and Saake.

No. 11. Lot No. 481. McKinney Bay, Placer County, California. Depth, 218 to 285 feet. Dec. 18, 1963. Fourteen asexual specimens and 1 fragment of *Phagocata*. Coll. Frantz and Saake.

No. 12. Lot No. 478. McKinney Bay, Placer County, California. Depth, 408 to 432 feet. Oct. 24, 1963. One sexual and 8 asexual specimens of *Phagocata*. Coll. Frantz and Keefer.

No. 13. Lot No. 470. McKinney Bay, Placer County, California. Depth, 415 to 423 feet. Feb. 19, 1963. Four asexual specimens and 2 fragments of *Phagocata*. Coll. Frantz and Wickwire.

No. 14. Lot No. 479. McKinney Bay and Sand Point, Placer County, California. Depth, 810 to 835 feet. Oct. 28, 1963. One sexual but not fully mature (No. 479a: slides) and 10 asexual specimens of *Phagocata*. Coll. Frantz and Arnold.

No. 15. Lot No. 454. Out from McKinney Bay, Placer County, California. Depth, 820 to 840 feet. Sept. 24, 1962. Three sexual (No. 454 b, c, d: slides) and 5 asexual (No. 454a: slides) specimens of *Phagocata*. Coll. Cordone and Frantz.

No. 16. Lot No. 469. Out from McKinney Bay, Placer County, California. Depth, 900 feet. Feb. 25, 1963. Two asexual specimens of *Phagocata*. Coll. Frantz and Davis.

No. 17. Lot No. 455. Out from McKinney Bay, Placer County, California. Depth, 1255 feet. Sept. 24, 1962. One sexual specimen (No. 455a: slides) of *Phagocata*. Coll. Cordone and Frantz.

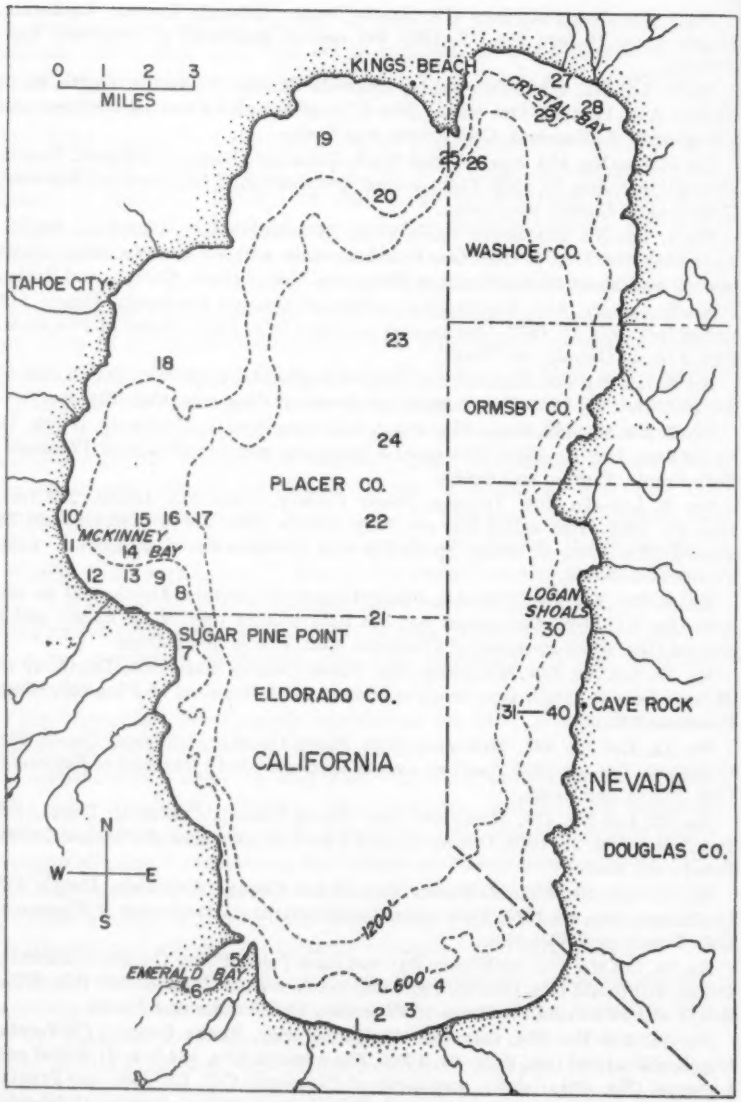

FIGURE 1.—Lake Tahoe, showing stations where planarians were collected (see "List of Localities").

No. 18. Lot No. 450. Tahoe City area, Placer County, California. Depth, 45 to 257 feet. July 24, 1962. Two asexual specimens and 2 fragments of *Phagocata*. Coll. Frantz, Curran, and Saake.

No. 19. Lot No. 458. Off Tahoe Vista, Placer County, California. Depth, 270 to 330 feet. Nov. 7, 1962. One sexual (No. 458a: slides—holotype) and 3 asexual (No. 458b, c: slides) specimens of *Phagocata*. Coll. Weidlein.

No. 20. Lot No. 459. Off King's Beach, Placer County, California. Depth, 474 feet. Five sexual (No. 459a, b, d, e: slides; No. 459f: whole mount—unfortunately broken through the atrial complex in transit) and 11 asexual (No. 459c: slides) specimens of *Phagocata*. Coll. Weidlein.

No. 21. Lot No. 483. Off Cave Rock and Secret Harbor (center of lake), Eldorado and Placer Counties, California. Depth, 1460 to 1582 feet. Dec. 4, 1963. Six sexual (No. 483a, b, c, d, e, f: slides) and 14 asexual specimens of *Phagocata*. Coll. Frantz and Davis.

No. 22. Lot No. 486. Off Logan Shoals and Secret Harbor (center of lake), Placer County, California. Depth, 1529 to 1583 feet. Oct. 28, 1963. Three sexual (No. 486a: slides) and 5 asexual specimens and 1 fragment of *Phagocata*. Coll. Frantz and Arnold.

No. 23. Lot No. 467. Between Skunk Harbor and Tahoe City (center of lake), Placer County, California. Depth, 1554 to 1623 feet. Dec. 14, 1962. Thirty-six asexual specimens (No. 467a, b, c: slides) and about 30 fragments of *Phagocata*. Coll. Frantz, Nicola, and Wickwire.

No. 23′. Lot No. 468. One sexual (No. 468a: slides—holotype) and 1 asexual (No. 468b, posterior piece: slides; No. 468b, broken head piece: whole mount) specimen of *Dendrocoelopsis*. (Same locality as No. 23.)

No. 24. Lot No. 485. Off Logan Shoals and Secret Harbor (center of lake), Placer County, California. Depth, 1566 to 1632. Aug. 27, 1963. Three sexual (No. 485a: slides) specimens and 2 fragments of *Phagocata*. Coll. Frantz and Davis.

No. 25. Lot. No. 465. Crystal Bay, Washoe County, Nevada. Depth, 65 feet. Dec. 13, 1962. One fragment of *Phagocata*. Coll. Frantz.

No. 26. Lot No. 466. Crystal Bay, Washoe County, Nevada. Depth, 250 to 444 feet. Dec. 20, 1962. One asexual specimen and 3 fragments of *Phagocata*. Coll. Frantz, Curran, and Saake.

No. 27. Lot No. 452. Crystal Bay, Washoe County, Nevada. Depth, 19 feet. Aug. 13, 1962. One asexual specimen of *Phagocata*. Coll. Frantz, Curran, and Saake.

No. 28. Lot No. 473. Crystal Bay, Washoe County, Nevada. Depth, 253 to 288 feet. June 26, 1963. Three sexual specimens and 1 fragment of *Phagocata*. Coll. Frantz and Saake.

No. 29. Lot No. 474. Crystal Bay, Washoe County, Nevada. Depth, 428 to 438 feet. June 26, 1963. Six asexual specimens and 1 fragment of *Phagocata*. Coll. Frantz and Zorko.

No. 30. Lot No. 451. Logan Shoals, Douglas County, Nevada. Depth, 618 to 630 feet. Aug. 16, 1962. One asexual specimen and 1 fragment of *Phagocata*. Coll. Frantz and Cordone.

No. 31. Lot No. 462. Cave Rock, Douglas County, Nevada. Depth, 24 to 70 feet. Dec. 19, 1962. Six asexual specimens (No. 462a: slides) and 2 fragments of *Phagocata*. Coll. Frantz, Curran, and Saake.

No. 32. Lot No. 447. Cave Rock, Douglas County, Nevada. Depth, 61 feet. July 16, 1962. One asexual specimen of *Phagocata*. Coll. Frantz, Curran, and Saake.

No. 33. Lot No. 480. Cave Rock, Douglas County, Nevada. Depth, 110 to 159 feet. Dec. 21, 1963. Ten asexual specimens of *Phagocata*. Coll. Frantz and Saake.

No. 34. Lot No. 457. Cave Rock, Douglas County, Nevada. Depth, 245 feet. Oct. 28, 1962. Three asexual specimens and 3 fragments of *Phagocata*. Coll. Frantz, Curran, and Saake.

No. 35. Lot No. 448. Cave Rock, Douglas County, Nevada. Depth, 290 to 325 feet. July 17, 1962. One, probably not fully mature, specimen of *Phagocata*. Coll. Frantz, Curran, and Saake.

No. 36. Lot No. 461. Cave Rock, Douglas County, Nevada. Depth, 299 to 415 feet. Dec. 19, 1962. Two asexual specimens and 2 fragments of *Phagocata*. Coll. Frantz, Curran, and Saake.

No. 37. Lot No. 482. Cave Rock, Douglas County, Nevada. Depth, 342 to 348 feet. Dec. 21, 1963. One sexual (No. 482a: whole mount) and 12 asexual specimens of *Phagocata*. Coll. Frantz and Saake.

No. 38. Lot No. 456. Cave Rock, Douglas County, Nevada. Depth, 422 feet. Oct. 28, 1962. Three asexual specimens of *Phagocata*. Coll. Frantz, Curran, and Saake.

No. 39. Lot No. 471. Cave Rock (Skyland), Douglas County, Nevada. Depth, 438 feet. May 13, 1963. One sexual (No. 471a: whole mount) and 3 asexual specimens of *Phagocata*. Coll. Frantz and Hauswald.

No. 40. Lot No. 476. Cave Rock, Douglas County, Nevada. Depth, 443 to 449 feet. Aug. 20, 1963. Two sexual (476a: slides) and 4 asexual specimens of *Phagocata*. Coll. Frantz and Zorko.

Family PLANARIIDAE

Genus *Phagocata* Leidy, 1847

Phagocata nivea tahoena, new subspecies

FIGURES 2, 3; PLATE 1

A large number of specimens of this planarian was collected from many stations of Lake Tahoe (see "List of Localities").

DESCRIPTION.—The appearance of this subspecies is shown in plate 1A–F. This is a slender, rather small pigmented species.[3] Sexually mature worms in a preserved condition are usually 5 to 8 mm long and 0.7 to 1.0 mm wide (largest specimens measured up to 12 mm in length), with the typical appearance of the genus *Phagocata*, i.e., with a truncate head without conspicuous auricles. There is no distinct narrowing behind the head. The body then gradually widens, reaching its greatest width at the level of the pharynx and copulatory apparatus. Behind the genital pore the body tapers to the moderately rounded posterior end.

[3] Regarding the color and size of the living specimens of the Lake Tahoe planarians, Mr. Ted C. Frantz informed me (in litt.) that "color varied from dark brown to translucent pink. The 'pink' were few in number and inhabited the bottom depth of the lake. They were also the largest of the planarians and approximately one-half inch or so in length." I consider his "dark brown" specimens to be *Phagocata nivea tahoena* and the "large translucent pink" specimens to be *Dendrocoelopsis hymanae*, described as a new species later in this paper.

The color of the dorsal side of the preserved specimens is usually a uniform grayish brown, that of the ventral side a light grayish brown. The situation of the pharynx and the copulatory apparatus may be marked by lighter pigmentation (pl. 1A–F). There are two eyes, situated close together (pl. 1G–I), each enclosed in a small, reniform clear space (pl. 1G). There is a pair of slightly visible auricular sense organs in the usual position (pl. 1G).

In mature worms the pharynx is situated behind the middle of the body and measures in length almost one-sixth the length of the body. In histological sections, it was observed that the internal muscle zone of the pharynx consists of two layers, circular fibres, and longitudinal fibres (characteristic of the family Planariidae). The anterior trunk of the intestine bears five to eight lateral branches; each posterior trunk has 10 to 12 lateral branches and many short medial branches in both the pharyngeal and postpharyngeal regions.[4] In many large worms, one to two pairs of medial branches situated at the level of the genital pore are united and form intestinal anastomoses that are located dorsally. Their cavities are lined with the same epithelium as that of the usual intestine.

The arrangement of the parts of the reproductive system was seen translucently from the whole mount (fig. 2). The numerous small testes extend in lateral regions from the level of the ovaries almost to the posterior end of the body. Their position is predominantly ventral, below the intestinal branches. Behind the genital pore, they are also found between the two intestinal trunks. In the central cavity of each testis a tangled mass of spermatozoa is found. The two sperm ducts are first noticeable as thin-walled tubular expansions (sperimiducal vesicles) packed with sperm and lying on each side of the pharynx. They are found in a ventral position from the level of the posterior two-thirds of the pharynx to the penis bulb (pl. 1B).

The two ovaries are of moderate size and typical, each situated behind the first pair of lateral branches of the anterior intestinal trunk. Numerous mature ova occur in the ovaries of the mature specimens. Occasionally, a ball of sperm was seen in a small chamber or ampulla of the ovovitelline duct next to each ovary (i.e., in the seminal receptacle). The two ovovitelline ducts proceed posteriorly in a ventral position and form a common ovovitelline duct at the level of the genital pore. The greater part of the ovovitelline ducts receives the ducts of numerous yolk glands (or vitellaria), the bodies of which are scattered in the surrounding parenchyma.

[4] According to the original description of *Phagocata nivea* from Alaska, the species possesses 10 or 11 pairs of the branches in the anterior intestinal trunk and 21 to 27 lateral branches in each posterior intestinal trunk (Kenk, 1953, p. 165).

The copulatory apparatus is shown in sagittal view in figure 3. The general anatomy of the copulatory apparatus of the present new subspecies bears a great resemblance to that of the Alaskan subspecies, *Phagocata nivea nivea* (cf. my fig. 3 and Kenk, 1953, p. 167, fig. 21).

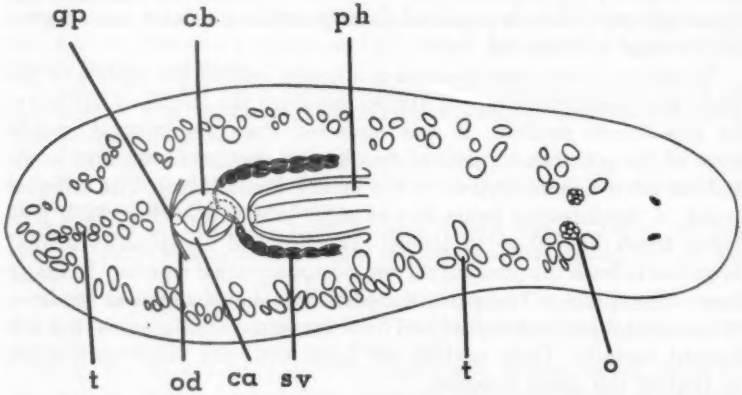

FIGURE 2.—General view of mature specimen of *Phagocata nivea tahoena* from whole mount: No. 459f.

The genital pore, situated in about the middle of the postpharyngeal region, leads immediately into a small cavity, the common antrum. This cavity leads to the left and dorsally into the canal of the copulatory bursa or the well-developed vagina, and to the right and anteriorly into the male antrum. The male antrum is wide anteriorly, tapering toward the genital pore, and its outer wall is lined with a rather tall, glandular epithelium. Below the epithelium there are two muscle layers, one circular and the other longitudinal. The narrow posterior part of the male antrum receives into its dorsal wall the common ovovitelline duct. Terminal portions of the ovovitelline ducts and the common ovovitelline duct are equipped with numerous eosinophilic cement glands.

The penis consists of two parts, a moderately large spherical bulb embedded in the parenchyma and a free, well-developed papilla projecting into the male antrum; the penis bulb is muscular. It contains a single bulbar cavity (seminal vesicle) from which a wide canal continues to the tip of the penis papilla. Typically, the penis lumen appears to be wider in the bulb than it is in the papilla, but no distinct ejaculatory duct is differentiated. The penis lumen is lined with an epithelium of glandular structure, tapering in thickness posteriorly. The penis bulb is pierced by numerous ducts of the penis glands, the

secretions of which pass into the bulbar cavity. Often the penis lumen and the male antrum are packed closely with this heavily eosinophilic granular secretion. The two sperm ducts enter the bulbar cavity from the anterolateral sides of the penis bulb separately.

The penis papilla has a symmetric conical shape when well extended but varies according to the degree of contraction. The outer wall of the penis papilla is lined with a flat epithelium, under which there are two muscle layers, a layer of circular fibres below the epithelium, and a layer of longitudinal fibres.

A slight morphological difference was noted in comparing the present new subspecies and *Phagocata n. nivea*. The new subspecies has a symmetric conical papilla with the opening of the penis lumen on its tip (fig. 3). The penis lumen of *Phagocata n. nivea*, however, opens ventrally at the tip of the papilla (Kenk, 1953, pp. 164–168, fig. 21). Kenk also notes that in "*Phagocata nivea* the penis lumen opens usually below the tip of the papilla" (p. 168).

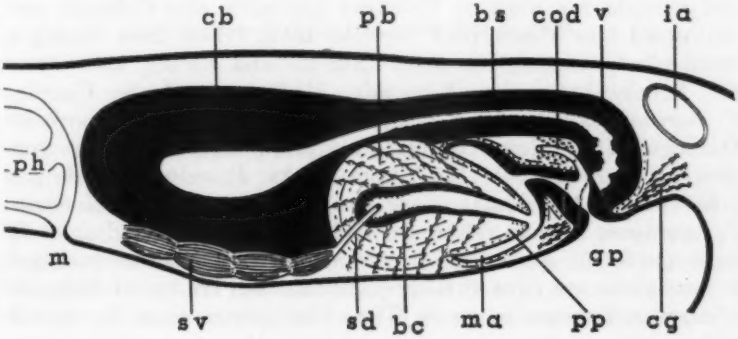

FIGURE 3.—Sagittal view of copulatory apparatus of *Phagocata nivea takoena*.

The copulatory bursa, which is situated in the usual position, is a large sac with somewhat irregular outline (fig. 3). The cavity of the bursa is lined with a very tall and thick glandular epithelium. In the lumen of this organ, in several worms examined, a mass of sperm was found enveloped in a coagulum of the secretion. The bursa stalk, a wide duct surrounded with a strong muscular coat consisting of intermingled circular and longitudinal fibres, runs posteriorly to the left of the midline, and curves ventrally to open to the common antrum (fig. 3). The posterior terminal part of the bursal canal becomes wide and forms the well-developed vagina. Numerous eosinophilic glands open into the common antrum near the genital pore.

In the lumen of the genital antrum in one of the worms examined (No. 460j), an undeposited cocoon was found. It was ovoid (0.8 x 0.5 mm) and a semitranslucent brown (pl. 1J).[5]

REMARKS.—The taxonomy of the genus *Phagocata* Leidy, 1847 (=*Fonticola* Komárek, 1926) has been discussed heatedly by several taxonomists such as de Beauchamp (1961), Dahm (1958), Darlington (1959), Hyman (1937a,b; 1951a,b), Ichikawa and Kawakatsu (1962a, b,c; 1963), Kenk (1930, 1935, 1944, 1953) and Kawakatsu (1965a). The genus as presently defined has representatives in Europe, Asia, and North America.

The indubitable North American *Phagocata* species are as follows: *Phagocata gracilis gracilis* (Haldeman, 1840) from Pennsylvania and Virginia westward to Missouri; *P. g. woodworthi* (Hyman, 1937a) from New England westward to the Delaware River (transitional forms between *gracilis* and *woodworthi* occur in New Jersey; see Hyman 1945, 1951b); *P. g. monopharyngea* Hyman (1945) from Iowa; *P. velata* (Stringer, 1909) from the Mississippi Valley, Michigan, and Ontario westward to Nebraska (probably also Colorado and southward into Missouri); *P. vernalis* Kenk (1944) from Michigan (midcentral states); *P. morgani* (Stevens and Boring, 1906) from the Appalachian region, Wisconsin, Michigan, and also Canada; *P. morgani polycelis* Kenk (1935) from Virginia; *P. bursaperforata* Darlington (1959) from Georgia; *P. oregonensis* Hyman (1963) from Oregon; *P. nivea* Kenk (1953) from Alaska; *P. subterranea* Hyman (1937b) from Donaldson's Cave and Mayfield's Cave of Indiana; *P. cavernicola* Hyman (1954) from Evac Cave of Pennsylvania. In these species (8 species and 4 subspecies) only *P. subterranea* and *P. cavernicola* are cave-dwelling planarians and are known from the subterranean waters in caves. The other species occur in epigean waters.

Externally, *Phagocata nivea tahoena* is readily distinguishable from all other North American *Phagocata* species except three, *P. velata*, *P. vernalis*, and *P. gracilis monopharyngea*, by the following points: size and form of the body, pigmentation on the dorsal side of the body, number of eyes, and number of pharynges. Anatomically, the arrangement and number of the testes and the structure of the copulatory apparatus of *P. n. tahoena* are distinctive.

Phagocata nivea tahoena differs from the other members of the genus in the following characters: small, up to 12 mm in the preserved state; head truncate without auricles; eyes two; colored; testes small, numerous, extending to the posterior end, lying ventrally; spermiducal

[5] After being photographed, the cocoon was mounted on a slide but unfortunately shrank into ridges. The head piece (the posterior part of the body had disintegrated) also was mounted on the same slide (No. 460j).

vesicles sacciform; sperm ducts entering bulbar cavity separately; penis bulb moderate in size and muscular; penis papilla conical; copulatory bursa large; bursal canal widened; common ovovitelline duct entering roof of posterior part of male antrum; one to two anastomoses of posterior intestinal trunks present; capsule oval.

HOLOTYPE.—One set of serial sagittal sections (No. 458a: 3 slides) will be deposited in the Division of Worms, Museum of Natural History, Smithsonian Institution, with four whole mounts (Nos. 459f, 471a, 482a, 460a: head piece and one cocoon) and 34 sets of serial sections (Nos. 446a, 454a-d, 455a, 458b,c, 459a-e, 462a, 463a,b, 464a-d, 467a-c, 475a-c, 476a, 479a, 483a-f, 485a, 486a). Some of these whole mounts and sections selected from the author's collection also will be deposited in that museum.

LOCALITY.—Lake Tahoe, Station No. 19 (holotype) and other stations at depths from 15 to 1632 feet.

Family DENDROCOELIDAE

Genus *Dendrocoelopsis* Kenk, 1930

Dendrocoelopsis hymanae, new species

FIGURE 4; PLATE 2

Only two specimens of this planarian, one mature and one immature, are available for this description. These were collected from the center of the lake (Station 23, depth 1554 to 1623 feet). As seen in plate 2A, B, a small part of the left side edge in the prepharyngeal region of the mature planarian was broken off; the immature specimen was broken in half near the pharyngeal base in transit (pl. 2C, D). These specimens were fixed but dried when received and were run up into a fluid of glycerin-alcohol for about two weeks. After taking photographs, I made serial sagittal sections of the mature specimen and the posterior piece of the immature specimen. The head piece of the immature specimen has been mounted on a slide and has broken into two fragments.

DESCRIPTION.—This is an unpigmented, eyeless species and measures up to 14 mm in length and about 2 mm in width in a preserved condition. The external appearance of both the mature and immature specimens is shown in plate 2A-D. The body form, however, especially the shape of the head, of a living worm is unknown.

The pharynx is situated behind the middle of the body. It is structurally typical of the family Dendrocoelidae: its internal muscular zone consists of intermingled circular and longitudinal fibres. The copulatory apparatus, which could be seen vaguely from the ventral side, occupies more than half the postpharyngeal region.

Externally the adhesive (or grasping) organ in fixed specimens (pl. 2B, D, E) is a well-developed concave ventral depression. On the basis of comparative observations on *Dendrocoelopsis ezensis* from Hokkaidô in northern Japan, the adhesive organ of *D. hymanae* is less developed than that of *D. ezensis*. The histological construction of the adhesive organ is illustrated in plate 2F. The subepidermal adhesive surface is covered with an epithelium devoid of rhabdites and pierced by numerous long gland ducts filled with a granular, eosinophilic secretion. The cell bodies of the glands are most numerous dorsally but also occur throughout the mesenchyme of the head region. The muscular system of this organ, which could not be analyzed in detail because of the poor histological condition of my slides and the density of the glandular structures, has fibres attached to the entire adhesive surface. This structure of the adhesive organ of the present species is very similar to that of the adhesive organ of *Dendrocoelopsis garnieri* (de Beauchamp, 1950, p. 69, fig. 2). Its muscular system is more weakly developed than in *Dendrocoelopsis spinosipenis* (Kenk, 1925, p. 133, fig. 2; Dahm, 1960, p. 16, fig. 9), or in *Dendrocoelopsis ezensis* (Ichikawa and Okugawa, 1958, p. 13, figs. 3, 4, pl. figs. 43–68) but more than in *Dendrocoelopsis vaginatus* (Hyman, 1935, p. 340, pl. 51: figs. 1, 2) and *Dendrocoelopsis vandeli* (de Beauchamp, 1932, p. 257, fig. 43).

The longitudinal strip of coarsely eosinophilic gland cells in each lateral margin is found in the present species; this character is common in many *Dendrocoelopsis* species (Ichikawa and Okugawa, 1958; Hyman, 1935; Kenk, 1925, 1953). It occurs both in the prepharyngeal region and in the posterior terminal part of the body (some sections of the body margin were lost) in the new species.

The anterior trunk of the intestine bears eight or nine pairs of lateral branches. Each posterior trunk has 13 or more pairs of lateral branches. The paired, rather large ovaries, situated behind the second pair of lateral branches of the anterior intestinal trunk, show no histological peculiarities. The ovovitelline ducts proceed backward and finally unite to form a short common ovovitelline duct at the anterior level of the genital pore and open into the male antrum close to the genital pore. The yolk glands or vitellaria, clusters of large and darkly stained cells, occur throughout the body length between the diverticula of the intestine.

The testes are moderate in size, numerous, and ventral in position. They are arranged in two zones on both sides of the midline, extending from the level of the ovaries to the base of the pharynx. In the central cavity of each testis occurs a tangled mass of sperm. The two sperm ducts form the usual sinuous tubes packed with sperm (the spermiducal vesicles) and are found from the level of about the middle of the

Phagocata nivea taboena, new subspecies (actual length 10–12 mm): A and B, no. 459f; C and D, no. 459a; E and F, no. 483a (a pair of normal eyes were found in the sections). Sketch of head of a preserved specimen: G, no. 454 group. Photomicrographs of head of preserved specimens from whole mounts: H, no. 459f; I, no. 460a. Cocoon: J, no. 460a (actual size 0.8 x 0.5 mm).

Dendrocolopsis hymanae, new species, preserved but dried specimens: A and B, sexually mature, no. 468a, holotype; C and D, sexually immature, no. 468b. Sketch of ventral side of prepharyngeal region: E, no. 468b. Median sagittal section through adhesive organ: F, no. 468a.

pharynx to that of the penis bulb. A sagittal view of the copulatory apparatus is shown in figure 4.

The genital pore opens immediately into two cavities, i.e., anteriorly into the male antrum containing the penis papilla and posterodorsally into the duct of the copulatory bursa. There is no division of the genital antrum into a common antrum and a male antrum (fig. 4). The opening of the common ovovitelline duct is situated in the roof of the terminal part of the male antrum. Terminal portions of the ovovitelline ducts and the common ovovitelline duct receive numerous glands, the secretion of which becomes a deep red when stained with eosin. The wall of the male antrum is lined with a cuboidal epithelium; the epithelium of the male antrum on the dorsal side is taller and more glandular than on the ventral. Under the epithelium there are two muscle layers, one circular and the other thick and longitudinal.

The penis consists of a large spherical bulb and a moderately large conical papilla; the bulb is very muscular. It consists of the usual mesh of muscle fibres taking a curved course paralleling the contours of the bulb. The penis bulb is pierced by numerous eosinophilic gland ducts that open into the bulbar cavity; these are seen easily in sections stained with Delafield's haematoxylin and eosin. The distinguishing feature of this species is the division of the bulbar cavity (seminal vesicle) into a pair of moderately wide, oval-shaped cavities in the penis bulb (fig. 4). The two continue to a narrow ejaculatory duct in the penis papilla.[6] Both the bulbar cavity and the ejaculatory duct are lined with a glandular epithelium of very tall cells, tapering in thickness toward the tip of the penis papilla. The two sperm ducts penetrate the penis bulb from the anterolateral sides and each opens into a cavity of the seminal vesicle.

The penis papilla has a slender and symmetric conical shape (fig. 4). It is covered with a tall epithelium similar to that lining the male antrum, under which there are two muscle layers, tapering in thickness toward the tip of the papilla: a layer of circular fibres containing a dense fibrous material next to the epithelium and a second layer of longitudinal fibres. The ejaculatory duct opens at the tip of the papilla.

The copulatory bursa is a large sac closely fitted into the space between the posterior wall of the pharyngeal chamber and the penis bulb (fig. 4). It has a narrow lumen and the internal wall is lined by a tall glandular epithelium. The bursa stalk runs posteriorly above

[6] In sagittal sections of the copulatory apparatus, the two parts of the separated bulbar cavity appear as if they are situated above and below the penis bulb rather than on either side of the midline of the body. This condition, however, seems to be the result of a postmortem muscular contraction, with a consequent listing to the side of the dorsoventral axis, through which the material was sagittally sectioned.

the penis, then curves ventrally and opens into the roof of the genital antrum. Its lumen enlarges distally; the epithelial lining of the lumen is thrown into villus-like folds. The muscle coat of the bursa stalk is well developed and consists of intermingled longitudinal and circular fibres. The walls of the distal part of the bursa stalk and the genital antrum near the genital pore are supplied with eosinophilous glands.

The egg-capsule or the cocoon of this species is not known.

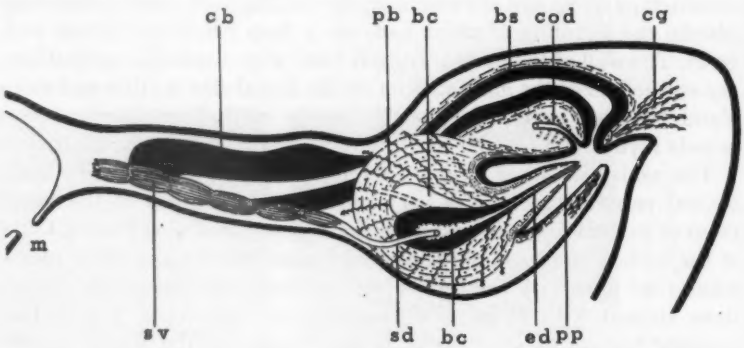

FIGURE 4.—Sagittal view of copulatory apparatus of *Dendrocoelopsis kymanae:* no. 468a.

REMARKS.—The genus *Dendrocoelopsis* was described originally by Kenk (1930). Afterward, Kenk (1953) modified the original definition of the genus by omitting the presence of a sucker as a generic character in order to include the species described under *Amyadenium* de Beauchamp. The taxonomy of *Dendrocoelopsis*, thus defined, was discussed by Hyman (1935), by Kenk (1953), by Ichikawa and Okugawa (1958), and recently by Dahm (1960). I am in complete accord with their opinions.

The species described under the genus *Dendrocoelopsis* (including *Amyadenium*) are as follows: *Dendrocoelopsis spinosipenis* (Kenk, 1925; possibly including *Digonoporus macroposthia* An Der Lan, 1941) from Yugoslavia, Sweden, and Denmark; *Dendrocoelopsis vandeli* (de Beauchamp, 1931), *D. brementi* (de Beauchamp, 1919) and *D. chattoni* (de Beauchamp, 1949) from the Pyrenees; *D. garmieri* (de Beauchamp, 1950) from central France; *D. brementi oculatum* (Porfirjeva, 1958) from the Caucasus; *D. lacteus* Ichikawa and Okugawa (1958) and *D. ezensis* Ichikawa and Okugawa (1958) from North Japan; *D. piriformis* Kenk (1953) and *D. alaskensis* Kenk (1953) from Alaska; *D. vaginatus* Hyman (1935) from Montana and Oregon in North America (Hyman, 1963).

Of the four known North American species of the genus (*D. piriformis, D. alaskensis, D. vaginatus,* and *D. hymanae*), only *D. piriformis* is a pigmented form, with two eyes and a well-developed adhesive organ. The Montana specimens of *D. vaginatus* are white and the Oregon (vicinity of Portland) specimens of the same species are dark, but microscopic examination shows that the dark color is caused by dark points in the cells of the entoderm (Hyman, 1963). This species has two eyes and an adhesive organ. *Dendrocoelopsis alaskensis* is also a nonpigmented form but without an adhesive organ. This species has two pairs of principal eyes.

Dendrocoelopsis hymanae differs from the other members of the genus in the following characters: moderate size, 14 mm in length (preserved), white, and eyes wanting; adhesive organ more developed than in *D. vaginatus*; testes prepharyngeal and ventral; penis bulb well developed; the seminal vesicle separated into two cavities (their positions are somewhat asymmetrical in my specimen) and sperm ducts entering separately; penis papilla conical, pointed, with single ejaculatory duct; copulatory bursa large; bursal canal thickened but less developed than in *D. vaginatus*; common ovovitelline duct entering the roof of the male antrum.

HOLOTYPE.—One set of serial sagittal sections (No. 468a: 11 slides) will be deposited in the Division of Worms, Museum of Natural History, Smithsonian Institution; also one whole mount of the head piece (No. 468b) and one set of sagittal sections of the posterior piece of the same specimen (No. 468b: 2 slides).

LOCALITY.—Lake Tahoe, Station No. 23′, at depths from 1554 to 1623 feet.

Ecological Notes

Lake Tahoe (fig. 1) is located in the Sierra Nevada Mountains at an elevation of 2097 m. It is 35.4 km long, 19.3 km wide, has a 114-km shoreline, a maximum depth of 548 m, and is the tenth deepest lake in the world. Water temperature of the lake is—offshore surface: maximum 20°C, minimum 5.5°C; at 67 m in depth: maximum 8°C, minimum 5°C.

Phagocata nivea tahoena and *Dendrocoelopsis hymanae* are the first recorded true lake-dwelling planarians in the United States. The former seems very common in the lake. Mr. Ted C. Frantz of the Nevada Fish and Game Commission informed me (in litt.) that "when we started our work on Tahoe we were surprised to find fairly large concentrations of planarians at various locations. Particularly so, when you consider Tahoe is relatively infertile. There has been some speculation as to their feeding habits on lake trout eggs." I was also much surprised to learn from the collector that a large number

of planarians that I had received were collected by the Ekman dredge method. According to my experience, *Bdellocephala annandalei* Ijima and Kaburaki, which inhabits Lake Biwa-ko in Middle Japan and is one of the largest freshwater planarians of the world, was taken easily with a dragnet used for *Chaenogobius annularis urotaenia* and *Gnathopogon elongatus*, but collection of this planarian hardly can be expected with the Ekman dredge (Kawakatsu, 1964). The chief food of *B. annandalei* is *Tubifex* worms inhabiting the muddy bottom of the lake (Gose, 1964).

Phagocata nivea from Alaska is an unpigmented epigean species with two eyes. It is a very interesting fact that a pigmented 2-eyed subspecies of *P. nivea* occurs in the bottom fauna of Lake Tahoe. In the North American freshwater planarian fauna, however, most of the *Phagocata* species are white, and so the absence of pigment in this genus cannot be regarded as adaptive (Hyman, 1954). *Phagocata bursaperforata*, which may be related to *P. morgani* and inhabits granite outcrops in Georgia, and *P. subterranea* from Indiana caves, which probably loses its eyes when adult, are the only white species without eyes in the genus. On the other hand, in the planarian fauna of the Japanese Islands, every subterranean *Phagocata* species known up to the present is white or translucent with two small eyes (*P. albata* Ichikawa and Kawakatsu, *P. tenella* Ichikawa and Kawakatsu, *P. papillifera* (Ijima and Kaburaki), *Phagocata* species Ichikawa and Kawakatsu of Tsushima Island), or translucent without eyes (*Phagocata?* species Ichikawa of Asahigawa, and several other undescribed forms). The Japanese epigean *Phagocata* species always are pigmented—*P. vivida* (Ijima and Kaburaki), *P. kawakatsui* Okugawa, *P. teshirogii* Ichikawa and Kawakatsu, *P. iwamai* Ichikawa and Kawakatsu (Kawakatsu 1960, 1965a, b).

A study of the present geographical distribution of planarian species of the world suggests that *Phagocata*, *Polycelis*, and *Dendrocoelopsis* are primarily Eurasian genera (Kawakatsu, 1965a). The chorology of species belonging to these genera has been discussed extensively: *Phagocata* species by Kenk (1943, 1953) and Kawakatsu (1965a), *Polycelis* species by Kenk (1952, 1953) and Kawakatsu (1965a), and *Dendrocoelopsis* species by Dahm (1960) and Kawakatsu (1965a). The occurrence of *Phagocata nivea tahoena* and *Dendrocoelopsis hymanae* in the Sierra Nevada Mountains may suggest that Alaska and the western area of the United States were populated by the proto-species migrating to these areas from Asia across the old land bridge on the Bering Strait (Kawakatsu, 1965a, fig. 10).

In the central and eastern states of North America, many species of the family Kenkiidae (consisting of the three genera: *Kenkia* Hyman, *Sphalloplana* de Beauchamp, and *Speophila* Hyman) have been

recorded from many caves. They are all white, eyeless cave-dwellers with an adhesive organ in the center of the anterior margin. The copulatory apparatus follows the plan of the genus *Phagocata*, from which the Kenkiidae presumably derive (Hyman, 1951b). In the Japanese Islands no specialized forms of planarians have been recorded from caves (Kawakatsu, 1960). The Japanese Islands are the continental islands of the Asiatic Continent and consist of younger strata than those of the North American Continent. Moreover, in the Neogene, the greater part of the Old Japanese Islands had sunk beneath the waves; this may have had a fatal effect upon the old Japanese flora and fauna (Kawakatsu, 1965a). On the other hand, a number of undescribed species belonging to the family Kenkiidae (probably *Speophila*) has been recorded from the subterranean waters in Middle Japan (Kawakatsu 1965a, b, c).[7] Knowledge is scanty concerning the Japanese subterranean water fauna although some troglobionts of the ancient type or preglacial relics—*Bathynella*, *Parabathynella*, *Allobathynella*, *Phreatodytes*, and *Morimotoa*—have been found in subterranean waters in the Japanese Islands (M. Uéno, 1960; S.-I. Uéno, 1957).

One of the speculations about the speciation of the genus *Phagocata* is that the members of the North American cave-dwelling Kenkiidae are the old immigrants to the New World, and at the same time a group more adapted to the cave habitat than those of the present North American *Phagocata* species. The speciation of the Japanese *Phagocata* species, which apparently originated from the Eurasian Continent, may not be so differentiated as the North American cave inhabitants except for a number of the above-mentioned true subterranean forms. More light could be thrown on this question by a more thorough study of the turbellarian fauna of the North Pacific areas of the Far East.

[7] Dr. Hyman kindly examined my photomicrographs of one of the forms that occurs in a well in Himeji City, near Ôsaka, Middle Japan (coll. Mr. Y. Morimoto).

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